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REVIEW

BIOGEOGRAPHY OF THE BRAZILIAN ATLANTIC FOREST: EVIDENCE FROM PHYLOGENETIC DATA SETS AND PERSPECTIVES FOR FERN AND LYCOPHYTE STUDIES

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Key words: Coastal Brazil, diversity, endemism, phylogeography, speciation.

ABSTRACT

Several biogeographic studies on plants and animals have focused on the Brazilian Atlantic Forest, a "hotspot" area for conservation. The majority of these investigations are on animals, and the most recent studies are based on molecular data (phylogeography). Geography of ferns and lycophytes has been a subject of study for a long time and the major papers involving plants from the Neotropics have been based on floristic surveys and taxonomic revisions. These revisions became more numerous about five decades ago. From the floristic surveys, the most important information is presence or absence of taxa in one area; from taxonomic revisions and other kinds of data, like elevational range, substrate preference, and dispersal capacity, additional clues can be found. New data sets from molecular studies, that have suggested hypotheses about fern and lycophyte evolution, have recently become available, but until now they remain largely underutilized. There is an enormous gap in the literature in using these new data to postulate evolution, radiation, and speciation in these groups of plants in South America. Here we present and discuss some of the recent molecular data for fern groups like *Lomariopsis*, *Pellaea viridis*, and *Megalastrum*. They corroborate the primary and secondary centres of diversity and endemism for ferns in tropical America as outlined by Tryon, and indicate that the Brazilian Atlantic Forest (coastal Brazil) and the Andes (from Venezuela to southern Bolivia) are special areas for evolution and speciation for ferns. Additionally, recent data show that the Brazilian Atlantic Forest has 834 species of ferns and lycophytes, of which 321 (approx. 38.5%) are endemics. An integrated evaluation from a phylogeographic perspective remains unexplored.

INTRODUCTION

Phylogeography could be considered a recent subdiscipline derived from traditional biogeography that deals with spatial and temporal dimensions of genealogy (Avise, 2009). The use of molecular data and temporal aspects to understand the origin, history, and evolution of organisms is a new paradigm for natural sciences. For Avise (2009), phylogeography differs from the traditional biogeography by its special focus on conspecific populations and on explicit genealogical information. Phylogeography differs from ecogeography by its special focus on historical causation in addition to the ecological processes.

To investigate phylogeography in animals scientists use mitochondrial DNA

(mtDNA), whereas in plants the principal molecular markers derive from chloroplast DNA (cpDNA). cpDNA occurs in many copies in the cytoplasm of a single cell, and most individuals show a single cpDNA haplotype sequence (i.e., are homoplastic). Individuals within the same species may have detectable differences in cpDNA sequence, which allows the use of plant cpDNA to estimate genealogical histories in plant population (Avise, 2009).

Brazil is one of the largest countries in the world, with an area of ca. 8.5 million km^2. As such it possesses the world's richest flora (40,989 species; 18,932 endemics; Forzza *et al.*, 2012) and is home to two biodiversity hotspots: the Cerrado and the Atlantic Forest (Myers *et al.*, 2000). Despite this importance, there is a paucity of biogeographic studies on Brazilian plants (Fiaschi and Pirani, 2009).

The Brazilian Atlantic Forest is considered one of the World's biodiversity hotspot areas because it contains a high percentage of endemic species and it is highly threatened (Myers *et al.*, 2000). This strip of forest occupies more than 4,000 km along the coast of Brazil (Figure 1), equivalent to the distance from Nova Scotia to Cuba (Thomas, 2008). Also, according to Thomas (2008), it comprises many types of forest, each with its own flora and today with particular conservation problems.

At least three hypothesized areas of endemism for plants have already been postulated for the Brazilian Atlantic forests, two of them located in the northeast and the other in the southeast (Prance, 1987; Thomas *et al.*, 1998). As pointed out by Thomas (2008), in Brazil the northeastern coastal forests can be found in six states (Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, and Bahia) and they differ from most of the forests in the states of Rio de Janeiro, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul, that comprise the southeastern portion of the Atlantic Forest. However, part of the forests in the states of Espírito Santo (at the Linhares Reserve) and Rio de Janeiro (Mata do Carvão) are treated as belonging to the northeastern portion of the Atlantic Forest, although they are outside the northeast area, because of their similarities to the forests of southern Bahia. The forests of the northeastern part of the Atlantic Forest are more accessible, more fragmented, and more diverse for flowering plants (Thomas, 2008), but less diverse for ferns and lycophytes (Prado and Sylvestre, 2010).

According to Batalha-Filho and Miyaki (2011), there are only a few publications on phylogeography of the Brazilian biota, and most have focused on animals and insects that occur in the Atlantic Forest, such as bees (Batalha-Filho *et al.*, 2010), frogs (Carnaval *et al.*, 2009; Thomé *et al.*, 2010), reptiles (Pellegrino *et al.*, 2005; Grazziotin *et al.*, 2006), birds (Cabanne *et al.*, 2007), and bats (Martins *et al.*, 2009).

For plant phylogeography, the main focus of the present review, Ribeiro *et al.* (2010) investigated *Dalbergia nigra* (Vell.) Allemão ex Benth., an endemic species from the central region of the Brazilian Atlantic Forest (Bahia refugium). They tested two hypotheses: 1) how the historical events of the Pleistocene influenced current genetic diversity and population structure of *D. nigra*; and 2) how forest fragmentation generated by human actions has affected the genetic diversity of populations. They identified three phylogeographic groups at different latitudes, and obtained evidence that the two northernmost groups maintained larger populations than the southernmost group. Vicariance (i.e., the splitting of one ancestral population into two or more populations, such as by continental drift or the formation of a geographic barrier; Simpson, 2006) plus climatic changes were identified as the main events for diversification of these groups in the Middle Pleistocene (ca. 350,000–780,000 y.a.). Comparisons among populations from large and small areas, as well as disturbed fragments of the same

phylogeographic group, showed anthropogenic effects on genetic diversity. Additionally, the authors concluded that the three phylogenetic groups can be considered three units, all of them needing special attention for preservation; together they represent a relict of the original genetic diversity of *D. nigra*.

Based on the results presented in these papers, Batalha-Filho and Miyaki (2011) compiled a map showing a recurrent result of the phylogeography of organisms along the Atlantic Forest of the Brazilian coast (Figure 1). There are three phylogeographic discontinuities (Figure 1A, B, C) for all studied groups related to glaciations and neo-tectonic activities during the Quaternary. The main hypothesis to explain these discontinuities is based on the Refugia theory (Haffer, 1969; Vanzolini and William, 1970; Brown and Ab'Sáber, 1979). This theory predicts that the wet dense forests, surrounded by dry and open vegetation, are islands (or refugia) for organisms. Also, according to this theory, the size of these forests changed significantly during late Quaternary climatic fluctuations (Pleistocene era). Wet forests retracted during the dry periods (forming the refugia) and expanded during the wet periods (inter-glaciation), whereas the dry vegetation showed an opposite behaviour.

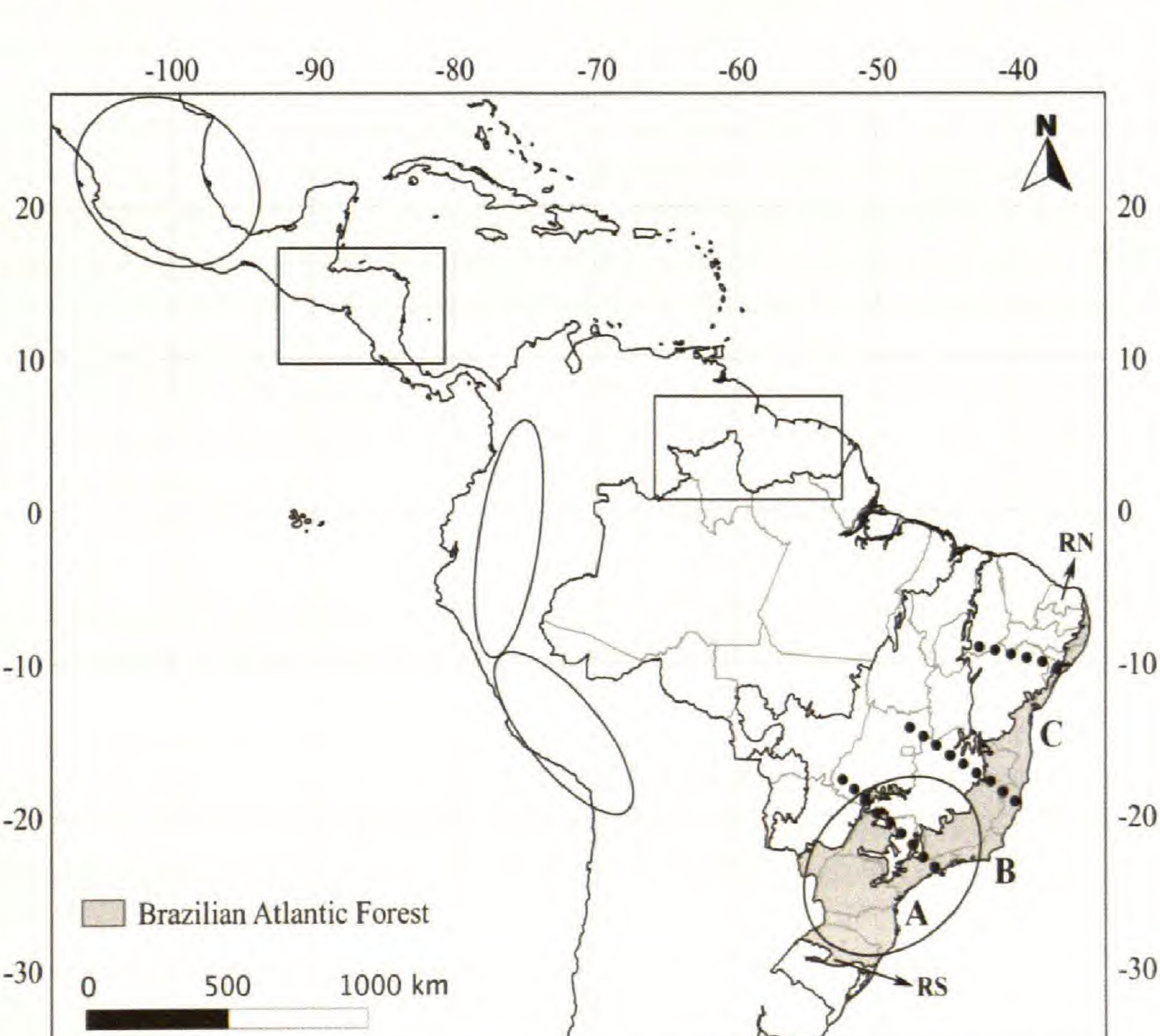

Figure 1. Primary (in circles) and secondary (in squares) centres of diversity and endemism for ferns and lycophytes in tropical America (based in Tryon, 1972). The letters A, B, C, represent the areas of refuges of the Quaternary along the Brazilian Atlantic Forest (based in Batalha-Filho and Miyaki, 2011). RN = Rio Grande do Norte State, RS = Rio Grande do Sul State.

Avise (2009) stated that phylogeography as a discipline has grown exponentially during the last 30 years. He commented on the necessity to improve the basic data for phylogeographic analyses, including evidence from the nuclear genome. According to the results by Edwards and Beerli (2000), increasing the number of loci is critical to decreasing the uncertainty in estimates of population time of divergence. The use of a single marker can lead to incorrect phylogeographic hypotheses, because the results may reflect the history of the chosen marker and not the history of the organism itself. The authors also commented that the use of different markers could result in different hypotheses. Brito and Edwards (2009) pointed out that the best way to reduce the coalescent stochasticity effect is to use several genetic markers, from both chloroplasts and nuclei (see details in Brito and Edwards, 2009; Kuhner, 2009).

Moritz *et al.* (2000), in their studies on diversification of rainforest faunas, stated that phylogeographic interpretation also depends on data about the biology of the species because the presence of a species in a niche is directly related to its ability to tolerate and survive extremes and variations of the environmental conditions during the maximum glacial periods.

Carnaval *et al.* (2009) published a good example of a study using molecular genetic data of three particular species of frogs, from distinct populations distributed along the Brazilian Atlantic Forest, to test hypotheses of how these different species populations responded to late Quaternary climate changes in South America and how these fluctuations helped to model present-day diversity. Besides traditional data for biogeographic approaches, they used a mitochondrial marker (mtDNA). The results revealed a hotspot within the Brazilian Atlantic Forest (the Bahian area). This place was a probable refugium for biodiversity during climatic extremes of the Late Pleistocene. The authors also commented that the genetic diversity and narrow endemisms in the central corridor of the biome (exactly in this area) have been greatly underestimated, because the collection efforts, molecular studies, and conservation priorities have been concentrated toward southern and southeastern Brazil. It is problematic since this part of the country has higher deforestation rates than in São Paulo State and southern Brazil (Carnaval *et al.*, 2009). At the end of this paper the authors presented a model to investigate biodiversity prediction. This model might be tested for some fern genera that speciated in this biome, like *Megalastrum*, various grammitid genera, *Serpocaulon*, *Campyloneurum*, *Pecluma*, *Pteris*, and others.

In addition to the molecular data and historical aspects to formulate phylogeographic hypotheses for ferns and lycophytes, two other important aspects need to be considered, the level of ploidy of the organisms and long-distance dispersal.

Haufler (2007) has commented on the importance of ideas published by Klekowski (1979) on polyploidy in ferns. He noted that for Klekowski: "… homosporous ferns could store variation among the several to many sets of chromosomes contained within single polyploid individuals. In effect, individuals could act as small populations, each containing considerable genetic variability, … even though individual sporophytes might originate through fertilization of genetically identical eggs and sperms (rendering them 100% *homologously* homozygous in a single generation) the variation introduced via the chromosome sets obtained through interspecific hybridization and subsequent polyploidy would perpetuate *homoeologous* heterozygosity". This mechanism has provided support for changes over time for homosporous ferns (Klekowski, 1979). Unfortunately, there are no data available of ploidy levels for ferns and lycophytes from Atlantic Forest.

Long-distance dispersal is a process that has been regularly investigated in the papers cited above, based on fern morphology, but has not been very well explored in recent phylogenetic papers that included plants from the Brazilian Atlantic Forest (e.g., Labiak *et al.*, 2010; Prado *et al.*, 2013), because they demand more population studies of each taxon to explain the current and previous pattern of geographic distribution.

Although Haufler (2007) summarized in a table the changes of perspectives about the studies of genetics, diversification, and biogeography of ferns, until now, only a few sets of data including these aspects on ferns and lycophytes are available and, consequently, only a few approaches can be used.

BIOGEOGRAPHY OF FERNS: A SHORT OVERVIEW

Several authors have discussed ideas about fern biogeography and speciation in tropical America, but there are no recent approaches using the available molecular data sets. According to Moran (2008), the earliest published works on fern and lycophyte biogeography (by d'Urville, 1835; Baker, 1868; Lyell, 1879; all cited by Moran, 2008) were based on numerical data only and involved percentages and/or occurrences of species in floristic regions around the world. These observations were amplified in subsequent publications by Christ (1910) and Winkler (1938), who detailed the floras by regions (see discussion in Moran, 2008). Copeland (1939) also published on biogeography, and the main focus of his views derived from the idea that ferns and lycophytes were ancestral in the Southern Hemisphere. Copeland concluded that most fern genera were of Antarctic origin (Moran, 2008), but his paper has been ignored by most recent pteridologists, because his assessment was too dogmatic (Moran, 2008). Since Copeland's work, several articles have been published by R. Tryon and others on fern biogeography.

Although his first ideas about biogeography dealt with the dynamic phytogeography of *Doryopteris* (R. Tryon, 1944), a representative group of ferns from the Brazilian Atlantic Forest, Tryon later published a series of papers dealing with speciation and biogeography of ferns and lycophytes (R. Tryon, 1970, 1971, 1972, 1985, 1986). Tryon's ideas about fern biogeography were based on data sets from several taxonomic revisions available. Some of these were published by him or his students (e.g., R. Tryon, 1941, 1942, 1956, 1976; Gastony, 1973; Windisch, 1977, 1978; Barrington, 1978), but some were by other authors (Alston *et al.*, 1981; Bishop, 1977, 1978; Copeland, 1952; Evans, 1969; Hauke, 1963, 1978; Kramer, 1957; Lellinger, 1972; Mickel, 1962, 1981; Morton, 1947; Murillo, 1968; Smith, 1971, 1974, 1980; Stolze, 1974); A. Tryon, 1957, 1962, 1970.

Tryon was especially interested in ferns and lycophytes occurring on isolated islands (R. Tryon, 1970). In this paper, he gave special attention to the processes of dispersal and migration of species to islands. He stated that these are complementary processes. The establishment of a species on an island is an individual event and it is closely related to the genetic variability of the species itself, because dispersal events cannot bring the entire genetic variability of a source population.

In his second paper, Tryon (1972) focused on plants growing on continents. He concluded that tropical American ferns are concentrated in three primary geographic areas: Mexico, the Andes, and Brazil (mainly Atlantic Forest). Two other secondary areas, Central America and the Guianas, were also discussed (Figure 1). Also according to Tryon, these regions contain 90% of the continental fern flora, of which ca. 60% are endemic to one particular region.

Smith (1972) also discussed several factors influencing fern distributions and categorized them as biotic (with a biological base) or as abiotic (with physical or chemical basis). He discussed the influence of each one and presented some cases of species distribution. Smith called attention to the distribution pattern between the Americas and Africa, and recorded a list of "species pairs" or species complexes occurring in both continents. In some cases, e.g., *Adiantum poiretii* Wikstr.*, *Asplenium auritum* Sw.*, *A. formosum* Willd.*, *A. lividum* Mett. ex Kuhn, *Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf.*, and *Trichomanes reptans* Sw.*, the species occur in both areas. Examples of species pairs are: *Asplenium feei* Kunze ex Fée*–*A. anisophyllum* Kunze, *A. serra* Sw.*–*A. friesiorum* C.Chr., *Blechnum schomburgkii* (Koltzsch) C.Chr.*–*B. tabulare* (Thunb.) Kuhn, *Elaphoglossum erinaceum* (Fée) T.Moore*–*E. hybridum* (Bory) Brack., *Microgramma lycopodioides* (L.) Copel.*–*M. mauritiana* (Willd.) Tard., and *Trichomanes radicans* Sw.–*T. giganteum* Bory ex Willd. The species marked with an asterisk occur in the Brazilian Atlantic Forest.

Moran and Smith (2001) amplified this list of species/species pairs in the Neotropics and Africa and presented more details about the species themselves, as well as the floristic affinities between both areas. To explain floristic affinities between the areas, they invoked long-distance dispersal, but at that time phylogenetic studies to support these examples were virtually non-existent. There were only a few groups for which molecular data existed (e.g., *rbcL*, for Vittariaceae; Crane *et al.*, 1995).

Furthering their studies, Tryon and Tryon (1982) identified four regions of the Neotropics with high species diversity and endemism: Greater Antilles, southern Mexico and Central America, Andean region, and southeastern Brazil. In each region ca. 40% of the species are endemics. The region of southeastern Brazil from the states of Minas Gerais and Espírito Santo south to Rio Grande do Sul contains about 600 species, mostly in the wet montane regions of the "Serra do Mar" (Tryon and Tryon, 1982). Some genera are especially diverse in this region and have several endemic species: *Doryopteris* (with 19 species) and *Anemia* subg. *Coptophyllum* (with 11 spp.) (Tryon and Tryon, l.c.). The Brazilian Atlantic Forest is considered to be one of the most important sites for conservation of biodiversity, and within this domain there are subregions with different levels of species composition, species richness, and endemism.

Salino and Almeida (2009) recorded 840 species to the Brazilian Atlantic Forest, and 269 of them are endemic (approx. 32%). The area included in this account, from the states of Rio Grande do Norte to Rio Grande do Sul (Figure 1), is larger than the area considered by Tryon and Tryon (1982) and that, in part, explains the different number of species.

More recently, Prado and Sylvestre (2010) published a full account of the Brazilian fern and lycophyte diversity. They recorded 1,176 species in the country, 123 spp. of lycophytes and 1,053 spp. of ferns. Among them, 450 spp. (38.2%) are endemic to Brazil (Figure 2). Most of the endemic species are distributed along the Brazilian Atlantic Forest (321 endemics of 834 spp.; 38.5%, Figure 2) (Forzza *et al.*, 2012). A full data set of the Brazilian diversity of plants and fungi can be found at the following website; these data are continually updated:
http://floradobrasil.jbrj.gov.br/jabot/listaBrasil/ConsultaPublicaUC/ConsultaPublicaUC.do

The most diverse Brazilian genera, with the number of endemic species, are summarized in Table 1 (based on Prado and Sylvestre, 2010). Genera with the highest percentage (> 55%) of endemic species in Brazil are: *Megalastrum*, with 18 species, 13 of which (72.2%) are endemic (Moran *et al.*, 2009a); *Huperzia s.l.*, with 38 species, 25

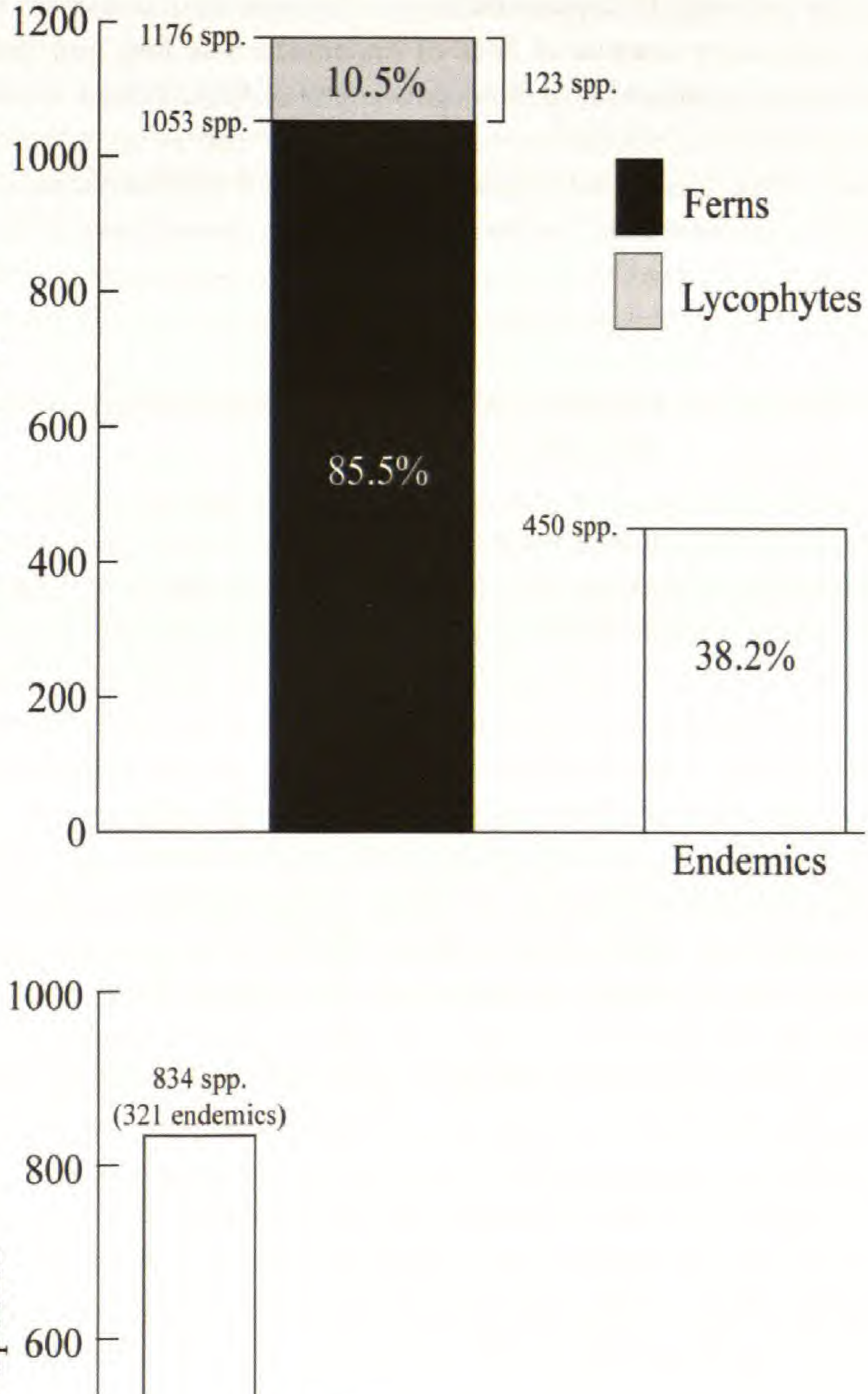

Figure 2. Diversity and endemism of ferns and lycophytes in Brazil and in their different types of vegetation. Source: Prado and Sylvestre (2010). (A.F.= Atlantic Forest; Am=Amazon; Ce=Cerrado; Ca=Caatinga; Pt=Pantanal; Pm=Pampa).

of which (65.8%) are endemic (Windisch, 1996); and *Doryopteris*, with 27 species, 16 of which (59.5%) are endemic (R. Tryon, 1942).

Despite these interesting numerical data of endemism and fern and lycophyte distribution, there are no publications on phylogeography of these groups of plants for South America in general, or for Brazil in particular. Does the endemism in these genera represent a radiation within the Atlantic Forest region, or does it represent many separate migrations of species into the region? In the next section we present some cases where the molecular data have helped to clarify taxonomic decisions about species delimitation or show interesting trends of speciation processes in the Brazilian Atlantic Forest.

RECENT MOLECULAR PHYLOGENTIC STUDIES INVOLVING BRAZILIAN FERNS

For the last two decades, phylogenetic papers involving ferns and lycophytes, based on DNA markers and morphology, have helped to elucidate the evolution and relationships among the major lineages of the ferns and lycophytes (e.g., Hasebe *et al.*, 1994, 1995; Pryer *et al.*, 1995, 2001; Korall and Kenrick, 2002, 2004; Schneider *et al.*, 2004; Schuettpelz *et al.*, 2007; Schuettpelz and Pryer, 2007; Rai and Graham, 2010). These general syntheses, as well as others, have stimulated the publication of new classification systems (Smith *et al.*, 2006, 2008; Christenhusz *et al.*, 2011a, b), and helped to address many long-standing questions about the taxonomic position for some groups, like the tree ferns, *Psilotum*, *Equisetum*, and the aquatic ferns. Concomitantly, new inferences about fern biogeography can be made, e.g., on origin of genera (Schneider *et al.*, 2007), origin of floras (Geiger *et al.*, 2007), and on diversification of a particular group in a given area (Polypodiaceae in Africa: Janssen *et al.*, 2007; cheilanthoid ferns in Cape region: Eiserhardt *et al.*, 2011).

More specifically for South America, there are no general papers dealing with origin of genera or floras, diversification of fern groups, or species radiations. However, there are a few examples that can be extracted from recently published phylogenies for a few genera or species that can serve as a first step for further investigations.

Lomariopsis is an example of a pantropical genus with species occurring in America and Africa/Madagascar (Moran, 2000; Rouhan *et al.*, 2007). According to the phylogeny of this genus, based on chloroplast intergenic spacer *trnL-trnF*, the *Lomariopsis sorbifolia*-group is entirely neotropical and another small group within this group, the *Japurensis*-group, occurs in the Neotropics and Paleotropics, forming monophyletic lineages in both regions. Within the *Japurensis*-group, the neotropical clade, formed by *L. marginata* (Schrad.) Kuhn, *L. prieuriana* Fée, *L. latipinna* Stolze, *L. nigropaleata* Holttum, and *L. japurensis* (Mart.) J.Sm., nests within a subclade formed by two African species, *L. guineensis* (Underw.) Alston and *L. palustris* (Hook.) Mett. ex Kuhn. The authors considered this nested relationship as a probable result of long-distance spore dispersal from the Neotropics to Africa, rather than as a result of continental drift (Moran and Smith, 2001). Morphological evidence of this relationship is the presence of long-spined spores in both African species. This kind of spore ornamentation is not found in other African species of *Lomariopsis*, but is present in *L. prieuriana*, a neotropical species. *Lomariopsis* shows evidence of local diversification in both New and Old Worlds (Haufler, 2007), and the combined data suggests that some African species have an ancestor in the Neotropics. Unfortunately, until now, this hypothesis has not been investigated in detail since publication of the first data set. This genus has one endemic species in the Brazilian Atlantic forest (*L. marginata*) that could be postulated as the

Table 1. Most diverse genera in Brazil and number of endemic species.
Source: Prado and Sylvestre (2010, updated in June 2013).

Genera	Total of species	Number of Endemic species (and %)
Thelypteris	87	47 (54.0)
Elaphoglossum	82	37 (45.1)
Asplenium	74	23 (55.4)
Anemia	70	41 (58.5)
Adiantum	63	19 (30.1)
Selaginella	55	15 (27.2)
Phlegmariurus	39	25 (64.1)
Cyathea	35	20 (57.1)
Trichomanes	33	2 (6.1)
Hymenophyllum	29	8 (27.6)
Blechnum	29	8 (27.6)
Doryopteris	28	16 (57.1)
Lindsaea	27	5 (18.5)
Diplazium	23	9 (39.1)
Pteris	22	6 (27.3)
Campyloneurum	21	5 (23.8)
Isoetes	21	16 (76.2)
Pecluma	19	8 (44.4)
Megalastrum	18	13 (72.2)
Microgramma	18	1 (5.5)
Ctenitis	17	10 (58.8)

putative ancestor of the radiation of the genus to Africa by vicariance or long-distance spore dispersal. Or the ancestor could be another species that belongs to the *Lomariopsis sorbifolia*-group.

For species with a disjunct distribution between America and Africa, Prado *et al.* (2013) studied a species pair, mentioned previously by Moran and Smith (2001): *Pellaea flavescens* Fée-*P. viridis* (Forssk.) Prantl. Moran and Smith had concluded that these two species are very similar but distinct, based on slight morphological differences. Prado *et al.* (l.c.), based on the analysis of plastid *rbcL* sequences, showed that *P. flavescens* from eastern Brazil is nested within the Old World species *P. viridis*, and the latter is the correct name for this taxon. However, its distributional history remains unsolved. Prado *et al.* considered two possibilities: 1) *P. viridis* may have been introduced in Brazil and subsequently naturalized; or 2) its occurrence in America is a natural result of long-distance dispersal, probably from Africa to Brazil.

Molecular evidence for *Megalastrum* (with 91 species, Moran *et al.* in prep.) is an excellent example of a genus with wide distribution and speciation processes in the Neotropics (Moran *et al.*, 2009a, b; Moran and Prado, 2010; Moran *et al.*, submitted), Africa/Madagascar (Rouhan and Moran, 2011), and circumaustral regions (Sundue *et al.*, 2010) (Figure 3). The Andean region contains the highest number of species in the genus (46 spp.) and the highest level of endemism (38 spp.; 83%) (Moran *et al.*, submitted). The Andean and the coastal Brazilian regions represent the primary centres of diversity and endemisms for *Megalastrum*. According to Moran *et al.* (2009a), *Megalastrum* in Brazil is represented by 18 species and 13 (72%) of them are confined

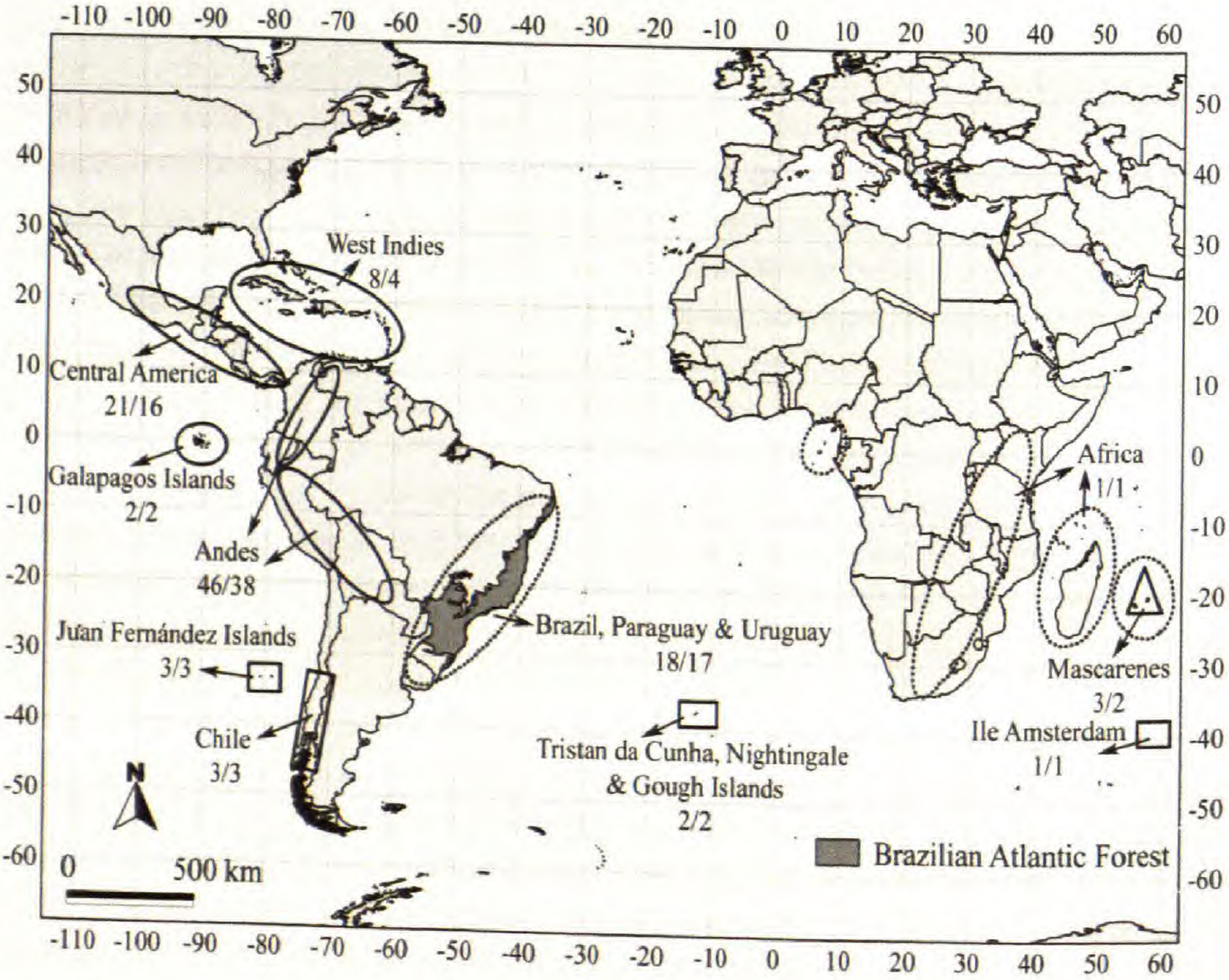

Figure 3. Diversity and distribution of *Megalastrum* in the world. Note the proportion of endemism in Brazil and the Andes (the number at left is the total number of species; the number at right side is the number of endemic species in the area).

to the Brazilian Atlantic Forest (the genus is absent from the Amazon Forest). Within this forest, some species show narrow endemism, such as *M. littorale* R.C.Moran *et al.*, *M. indusiatum* R.C.Moran *et al.*, *M. organense* R.C.Moran *et al.*, *M. substrigosum* R.C.Moran *et al.*, and *M. retrorsum* R.C.Moran *et al.* All of these Brazilian species appear in the same clade in multiple analyses. These species represent a lineage that diversified in the Brazilian Atlantic Forest.

Despite the importance of the South American flora, and the available data sets from literature and herbarium collections, none of the molecular papers here cited have postulated new ideas about the origin or diversification of the studied groups in the Neotropics; however, the data suggest an important process of diversification in the Brazilian Atlantic Forest.

FURTHER INVESTIGATION

Phylogeographic studies involving ferns and lycophytes are potentially important to show that these groups can be used as confident indicators to prioritize areas for protection and conservation of the Brazilian Atlantic Forest, a relictual biota and a hotspot area of biodiversity. Such studies are now feasible because there are several data sets already available for the groups such as, e.g., the high percentage of endemic species and their distribution (Forzza *et al.*, 2010 plus subsequent updates), recent molecular data for some genera and species, as well as biogeographic data that can be taken from taxonomic revisions of the genera or groups of species.

However, to improve the data sets we need the following: further phylogenetic monographs of genera to identify common or putatively ancestral lineages within genera or group of species; studies of groups known or thought to comprise elements in both Africa and South America, or other areas; more studies of older lineages like filmy ferns; better integration of climatic/paleobotanical data with phylogenetic data; more populational studies of particular groups to understand the current and previous geographic distribution, and determination of ploidy level in the Brazilian plants.

For the Brazilian Atlantic Forest several groups (with many endemic and/or widely distributed species) can be investigated following this new paradigm, and among them we suggest: *Asplenium*, *Ctenitis*, *Cyathea*, *Doryopteris*, *Elaphoglossum*, and *Thelypteris* (ferns), *Isoetes* and *Phlegmariurus* (lycophytes) (see Table 1).

As already commented by Moran (2007), recently several new sources of information about fern phylogeny have accumulated, and this set of data affects interpretations of distance dispersal versus continental drift in explaining intercontinental relationships. The intercontinental disjunctions between Brazil and Africa are particularly interesting, but the absence of data from the Brazilian ferns and lycophytes imposes barriers for new interpretations about these distributions. Most of the taxa involved in these kinds of disjunctions between Brazil and Africa are from different regions of the Brazilian Atlantic Forest (see examples given above). Molecular studies based on DNA samples from different populations of these species, allied to the molecular clock methods, are necessary for better understanding and clarification of these patterns of species distribution. Unfortunately, phylogeographic studies on ferns and lycophytes from Brazilian Atlantic Forest are not in progress and this field of research remains unexplored.

Another interesting aspect to be investigated relates to the particular patterns of distribution of fern and lycophyte species along the Brazilian Atlantic Forest. Further examination of these lineages in a phylogenetic context will help to clarify the micro-endemism found in some genera, the high percentage of endemism in general for

these groups as well as whether the actual scenario is the result of isolated speciation events or species radiations processes. However, the last two points need to be studied using temporal information and robust phylogenetic hypotheses (Schneider *et al.*, 2010).

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ASPLENIUM AURITUM SW. *SENSU LATO* (ASPLENIACEAE: PTERIDOPHYTA) - AN OVERLOOKED NEOTROPICAL FERN NATIVE TO THE AZORES

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Key Words: Drouet, Eared Spleenwort, Flores, Macaronesia, neotropical element

ABSTRACT

Asplenium auritum Sw. *sensu lato* (Eared Spleenwort) is recorded for the Azores and the Macaronesian region for the first time. Misidentified herbarium specimens indicate it to have first been collected on Flores by Drouet in 1857, strongly supporting a native status. A member of a critical species complex of sexual and apogamous lineages of various ploidy levels and widely distributed in Central and Southern America, the Caribbean, Madagascar and eastern Southern Africa, we consider this represents another example of a neotropical element naturally present in the Azorean flora. The taxonomy of this group is far from resolved. It is still unclear whether the Azorean material can be definitely identified with an existing named entity in this group or may be unique and endemic; further molecular work is needed to resolve this issue. Currently fewer than 50 individuals are known from one small area where it is highly vulnerable to both development and collection; we therefore suggest an IUCN category of Critically Endangered – CR (B1,2 a &b, D).

INTRODUCTION

The Macaronesian region, comprising the North Atlantic volcanic, oceanic archipelagos of the Azores, Madeira, Selvages, Canaries and Cape Verdes (Figure 1a) is recognised as a Biodiversity Hotspot with a rich endemic flora (Schaefer, 2003a) and as a globally important centre for pteridophyte diversity. In the Azores, the most northerly and isolated archipelago of the region, comprising nine islands located 1600 km west of the Iberian peninsula, pteridophytes form a notable component of the vegetation. In spite of this interest, the flora remains under-worked and patchily recorded (Schaefer *et al.*, 2011). This is perhaps particularly true of Flores and Corvo (Figure 1b), the two westernmost islands of the Azores, where several previously overlooked pteridophyte taxa, some widely disjunct (Schaefer, 2001, 2003, Rumsey & Schaefer, in prep.), have recently been identified.

During the course of collaborative fieldwork in July-August 2008 between botanists from the Natural History Museum, London (FJR/MC) and those from project "Veronica" at the University of the Azores, a distinctive *Asplenium*, unlike any currently recorded for

Macaronesia (Hansen & Sunding, 1993), or Europe (Tutin *et al.*, 1993), was found in two discrete patches less than 100 m apart. The plants occurred on old walls by tracksides in *Pittosporum*-dominated woodland close to the small village of Cuada on the west coast of Flores (Fig 1c). A return visit to the area by HS in June 2011 detected plants in two patches at another locality, in similar habitats and vegetation, and all within the same square kilometre.

On first sight, the coriaceous texture, channelled rachis and colour suggested a possible hybrid involving *Asplenium marinum* L., of which none are currently known, but the absence of the putative parent, plus the number of individuals of varying age and maturity made this unlikely, and the plant's production of well-developed spores quickly ruled this out. Even though present in small quantity the plants found showed considerable variation in morphology, with the 2011 populations demonstrating that the

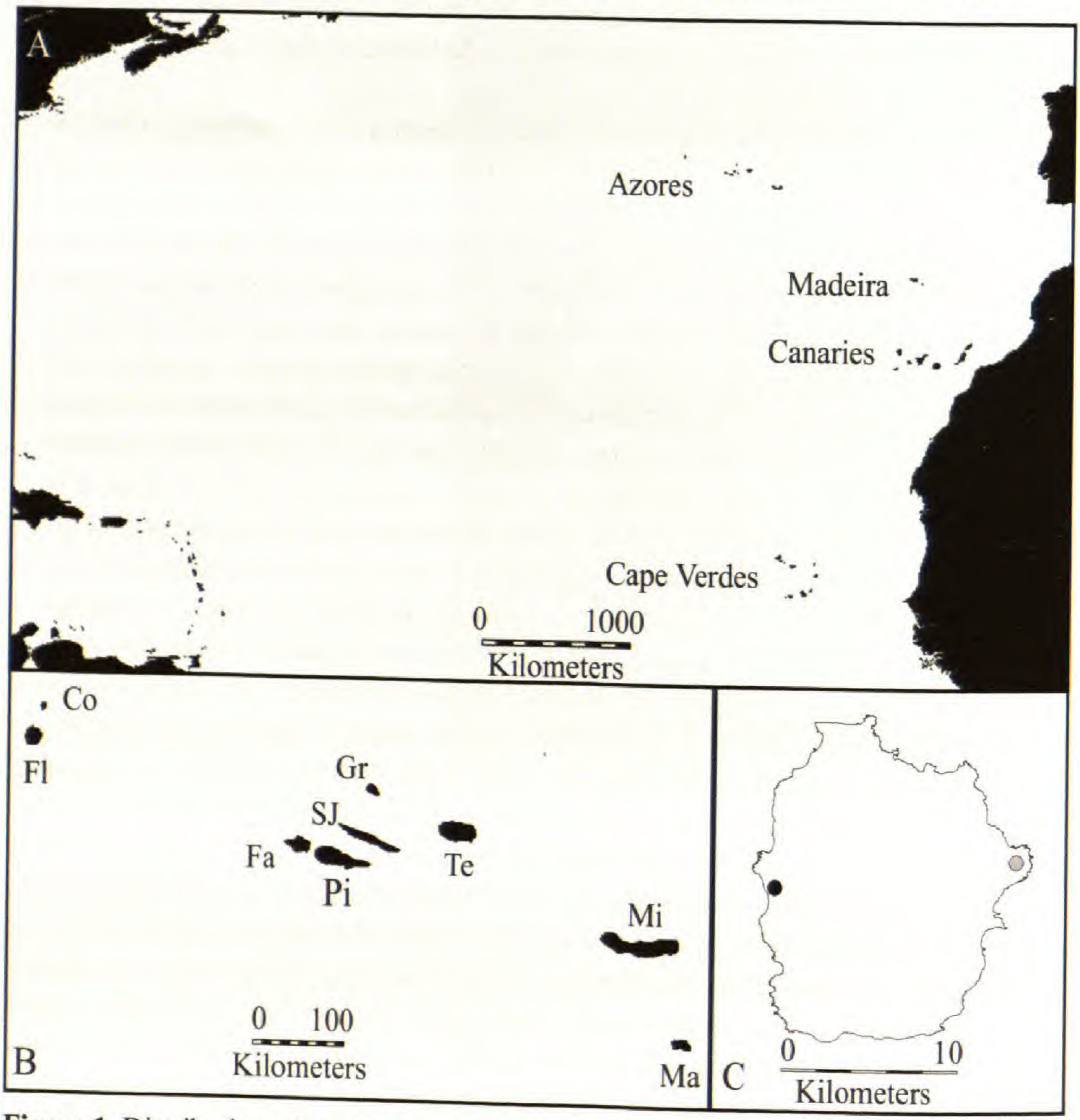

Figure 1. Distribution of *Asplenium auritum* in the Azores. **A.** The location of the Azores in relation to the other Macaronesian archipelagos (Madeira, Canaries, Cape Verdes) and continental landmasses. **B.** The nine islands of the Azorean archipelago. Fl = Flores; Co = Corvo; Fa = Faial; SJ = São Jorge; Pi = Pico; Gr = Graciosa; Mi = São Miguel; Ma = Santa Maria. **C.** The island of Flores showing the location of Aldeia da Cuada (black circle) where all localized collections of *A. auritum* have been made and Santa Cruz das Flores (grey circle) where Drouet probably collected the species on August 3rd 1857 (see text)

juvenile frond form differed significantly in dissection (Figure 2).

Given the floristic links demonstrated by other cryptogamic taxa in the Western Azores (Vanderpoorten *et al.*, 2007) it was considered that related or taxa identical to the novel *Asplenium* should initially be sought from the floras of the Caribbean, Central America and southern North America. Using the keys in Wagner *et al.*, (1993), Adams (1995) and Proctor (1985), the material was quickly identified as belonging to *Asplenium auritum* Sw. *sensu lato*.

The *Asplenium auritum* complex is widely distributed, occurring in both the Neo-tropics and Palaeo-tropics. The centre of diversity and abundance would appear to be in Central and South America, from Brazil to Bolivia, with populations scattered northwards to southern Mexico, finally reaching a northern limit in Florida, where it is listed as Endangered (E) by the Florida Department of Agriculture. There it occurs primarily as an epiphyte on old oaks (*Quercus virginiana* Miller) in low altitude (<50 m), shady forests (Wagner *et al.*, 1993). It was long thought to be restricted to a single site in Sumter County but has since been detected in small quantities in a further seven counties, although now perhaps extirpated in Dade County (Nelson, 2000). The Florida plants are morphologically dissimilar from the Azorean in their narrower and more acute pinnae. Interestingly, Lakela and Long (1976) regarded the plant as an introduction from Jamaica. *Asplenium auritum sensu stricto* occurs relatively commonly within Jamaica and through the Greater Antilles where it is present at middle elevations (275-945 m), primarily as an epiphyte in humid woodlands, more rarely on banks or humus-filled pockets in rocks (Proctor, 1985). *Asplenium auritum* var. *bipinnatifidum* Kunze (which Proctor (1985) equates with *A. rigidum* Sw.) is also present but additionally distributed through the Lesser Antilles and Trinidad and occurring at higher altitudes (518-1220m). The species aggregate also occurs, but rarely, in La Réunion and Mauritius in the Mascarenes (Autrey *et al.*, 2008) at altitudes up to 1400m, growing in primary woodlands and ravine streambeds. In south-eastern Africa the aggregate is found from 650-1220m in warm, tropical, semi-deciduous woodland and riverine forest along the foot of the eastern escarpment of Zimbabwe, extending into western Mozambique; it is also reported in Malawi and the People's Republic of Congo (Burrows, 1990). Usually plants occur as epiphytes at low altitudes but also as lithophytes, more rarely terrestrial, on earthy banks in light shade. Plants of this aggregate also occur in the forests of Central Madagascar. Christensen (1932) clearly had some doubts about the identity of this material which, although rare, showed considerable morphological variation, with plants being linked to both *A. macilentum* Kunze ex Klotsch and *A. rigidum*.Sw. From the limited material initially available and using the concepts and descriptions in Mickel & Smith, (2004) it was considered that the plant more closely approached *A. cuspidatum* Lam. (which those authors synonymised with *A. auritum* var. *bipinnatifidum*), and it was as such that the Flores plant was listed in Silva *et al.* (2010). The later gatherings by HS and the discovery of additional herbarium material has allowed a more considered judgement of the plant's identity to be made. Pending a full revision of the complex necessary to establish the identity of the Azorean material as either endemic to the archipelago or more widespread, we refer it to *A. auritum sensu lato,*. In this paper, we provide a description of *A. auritum* in the Azores, together with a key to the species of *Asplenium* in the Azores, to facilitate identification. The status, distribution, ecology and conservation status of Azorean *A. auritum* are also discussed, in light of our collections and those made by earlier collectors.

DESCRIPTION OF AZOREAN MATERIAL

Asplenium auritum Swartz, J. Bot. (Schrader). 1800(2): 52. 1801.

Rhizome erect, unbranched; densely clothed at apex with scales; scales brown throughout, broadly linear, 1-2 × 0.7-1.1 mm, margins shallowly and widely dentate. Petiole green, sometimes blackish brown abaxially, dull, channelled, 2-10(-12) cm, 1/3-1/2 length of frond; indumentum absent. Blade narrowly deltate to lanceolate, degree of dissection variable: juvenile foliage finely 2-pinnate (Figure 2), mature fronds once pinnate-pinnatifid to 2-pinnate (Figure 3), 4-20(-30) × 1.8- 9cm, thick, somewhat coriaceous, glabrous; broadest at base, tapering gradually to apex. Rachis green, dull, channelled, +/- glabrous. Pinnae in 10-18 pairs, linear-deltate, medial pinnae 0.7-4.5 × 0.3-1cm; base with acroscopic auricle or pinnule enlarged, somewhat excavate in proximal 1/5-1/4; margins mostly obtusely lobed to dentate, pinnate proximally or in proximal 2/3; apex obtuse. Sori oblong, 4-9(-12) pairs per pinna, subcostal, nearly parallel to costae on both basiscopic and acroscopic sides, sometimes restricted to distal portion of pinna (Figure 4). Indusium membranous, entire. Spores somewhat variable in shape, reniform-elliptic rarely subglobose, perispore weakly cerebriform-reticulate, obscurely crested, sparsely echinulate, exospores 32-42.5 × 22.5-28(-30) µm.

Asplenium auritum can be discriminated from the other species of *Asplenium* in the Azorean flora by a unique combination of characters. A key to the Azorean taxa is presented below. Twelve species of *Asplenium* have previously been recorded; one, *A. ruta-muraria* L. was presumed to be an introduction that did not persist and it is not treated in the key. Another, the Macaronesian endemic *A. anceps* Hook. & Grev. is also known only from a single gathering, from Pico in 1973 (Lovis *et al.*, 1977). It is implicated in the origin of the Azorean endemic *A. azoricum* Lovis, Rasbach, K.Rasbach & Reichst. (Rumsey *et al.*, 2004) and may be overlooked for that species and so is

Figure 2. *Asplenium auritum* Sw. Cuada, Flores, June 2011 showing dissected juvenile foliage and once pinnate-pinnatifid fronds of young mature plants. Photo. H. Schaefer

Figure 3. *Asplenium auritum* Sw. Cuada, Flores, June 2011 showing increasing levels of frond dissection on mature plants. Photo. H. Schaefer

Figure 4. *Asplenium auritum* Sw. Coada, Flores, June 2011 - undersurface of mature fronds showing indusial arrangement. Photo. H. Schaefer

included. Six hybrids have been reported, a seventh (*A. onopteris* L. × *A. obovatum* Viv. subsp. *lanceolatum* (Fiori) P.Silva) is believed to occur but has yet to be confirmed cytologically (Rumsey, in prep.). Of these six, one has only been found once: *A. azoricum* × *A. scolopendrium* L. (Rumsey *et al.*, 2004), while the majority are apparently very infrequent but perhaps overlooked: *A. azoricum* × *A. trichomanes* subsp. *quadrivalens* D.E.Mey. has been recorded on Terceira and Sao Miguel (Rumsey, in prep.); *A. onopteris* × *A. scolopendrium*, while lost from Faial (Schaefer & Rasbach, 2000) has now been found in several sites on Santa Maria (Schaefer, 2003b). Of the other three hybrids, *A. azoricum* × *A. onopteris* is currently also known only from Santa Maria but again has been found in several sites there (Rumsey *et al.*, 2004), *A. adiantum-nigrum* L. × *A. obovatum* subsp. *lanceolatum* is known from Pico, where first recorded by Bennert *et al.*, (1992) and the last, *A. adiantum-nigrum* × *A. onopteris*, is more widely distributed, overlooked and apparently often more frequent than *A. adiantum-nigrum* itself (Schaefer, 2003c). All hybrids are intermediate between their parents and show high levels of sterility, manifested in the production of misshapen, abortive spores.

Key to the Azorean species of *Asplenium*

1. Fronds entire 2
   Fronds pinnate-pinnatifid 3
2. Frond blade as wide as long, with acute lobes ..... *A. hemionitis* L.
   Frond distinctly longer than wide, unlobed ..... *A. scolopendrium* L.
3. Frond simply pinnate 4
   Frond pinnatifid to twice-pinnate 9
4. Rachis with distinct abaxial wing ..... *A. anceps* Lowe
   Rachis without distinct abaxial wing 5
5. Fronds not coriaceous, rachis without distinct adaxial channel 6
   Fronds coriaceous, rachis distinctly channelled 8
6. Pinnae entire with single basiscopic sorus ..... *A. monanthes* L.
   Pinnae crenate with >2 sori 7
7. Pinnae >2 × as long as wide, distinctly crenate, glossy ..... *A. azoricum* Lovis, Rasbach, K.Rasbach & Reichst.
   Pinnae <2 × as long as wide, indistinctly crenate, matt ..... *A. trichomanes* L. subsp. *quadrivalens* D.E.Mey.
8. Frond broadest at base, narrowly triangular ..... *A. auritum* Sw.
   Frond parallel sided, often widest above middle ..... *A. marinum* L.
9. Basal pinnae much shorter than those in mid frond ..... *A. obovatum* Viv. subsp. *lanceolatum* (Fiori) P.Silva
   Basal pinnae ± the longest 10
10. Frond coriaceous, lower pinnae with acroscopic auricle ..... *A. auritum* Sw.
    Frond not coriaceous, pinnae never auriculate 11
11. Ultimate segments narrowly lanceolate, acute at base, mean exospore length <30 µm ..... *A. onopteris* L.
    Ultimate segments lanceolate, somewhat obtuse at base, mean exospore length >30 µm ..... *A. adiantum-nigrum* L.

SPECIMENS SEEN

Asplenium auritum Sw. Azores, Portugal, Flores Island. walls of track leading NE from Casa do Espirito Santo, Aldeia do Quada UTM 0650034/4367245, alt. 146 m asl. Leg.

Carine *et al.*, 58, 8 July 2008. BM
Asplenium auritum Sw. Azores, Portugal, Flores Island. walls of track leading NE from Casa do Espirito Santo, Aldeia do Quada UTM 0650003/4367488, alt. 137 m asl. Leg. Carine *et al.*, 60, 8 July 2008. BM
Asplenium auritum Sw. Azores, Portugal, Flores Island. *Pittosporum undulatum* forest near the village of Cuada (Fajã Grande). UTM 0650180/4367706, alt. 128 m asl. Leg. Hanno Schaefer 2011/405, 17 June 2011. BM
Asplenium auritum Sw. Azores, Portugal, Flores Island. *Pittosporum undulatum* forest near the village of Cuada (Fajã Grande). UTM 0650185/4367697, alt. 135 m asl. Leg. Hanno Schaefer 2011/406, 17 June 2011. BM

Examination of herbarium material at BM revealed two further gatherings of this taxon. One was made in the same area as the recent finds, near the small village of Cuada (Coada/Quada) above Fajã Grande, by C. M. Ward in July 1967 (Figure 5). This specimen (Ward 24) was not mentioned by Ward (1970) in his account of the pteridophyte flora of the island and remained undetermined until incorrectly identified as *A. obovatum* subsp. *lanceolatum* by Ormonde in 1992. The second, much older specimen (Figure 6), was collected by Drouet on 3 August 1857 and is localised only to the island "Flores". Drouet's account of his visit to the Azores (Drouet, 1866) indicates that he was present on Flores from 28th July through to the date on which he collected this specimen (3rd August). His reported itinerary shows he never visited the western coast and the Fajã Grande area in which all recent finds have been made. On 3rd August he was preparing to move on to Faial, and so confined his activities to areas immediately adjacent to Santa Cruz on the east coast, then, as now, the most populous and developed area on the island. He initially labelled the plant as "voisin du *marinum*" (ie *A. marinum*), which in frond texture and colour is indeed the most similar Macaronesian/European species but which never shows the bipinnate dissection of Drouet's plant. Subsequently the specimen was incorrectly labelled as "*Asplenium adiantum-nigrum* L *forma forsam ad* II. *C. onopteris* Heufl. *A acutum* (Bory) Milde" [= *A. onopteris* L.]

ECOLOGY

Asplenium auritum is restricted to low-altitude forest within the Azores, the finds near Cuada made between 125 - 200 m. No altitude is given by Drouet but, given his known movements on the day he collected the specimen, the site would be no higher than at Cuada and perhaps much closer to sea-level. This zone has seen the most profound change since the arrival of settlers in the 15th and 16th centuries, with woodland and scrub clearance and the replacement of the dominant species by alien and invasive taxa. Structurally however, this latter-day vegetation may not be entirely dissimilar to the original, and many native cryptogams of the understory appear to have survived in sheltered and ravine sites. For instance, *Culcita macrocarpa* C.Presl recruits abundantly in some areas on the fibrous trunks of the Asian *Cryptomeria japonica* (L.f.) D.Don in old forestry plantations. The species grows in secondary scrubby woodland, dominated by the invasive *Pittosporum undulatum* Vent., and in moderately exposed to rather deeply shaded conditions on dry stone walls made of the local volcanic rock which border the trackways; these are usually free-standing but sometimes soil-backed. Here it occupies the somewhat soil-filled interstices between the blocks, or where soil and humic debris accumulates on the block's pitted oblique and near horizontal surfaces. It is closely associated with very few vascular species, predominantly pteridophytes such as *Polypodium macaronesicum* Bobrov subsp. *azoricum* (Vasc.) F.J.Rumsey, Carine &

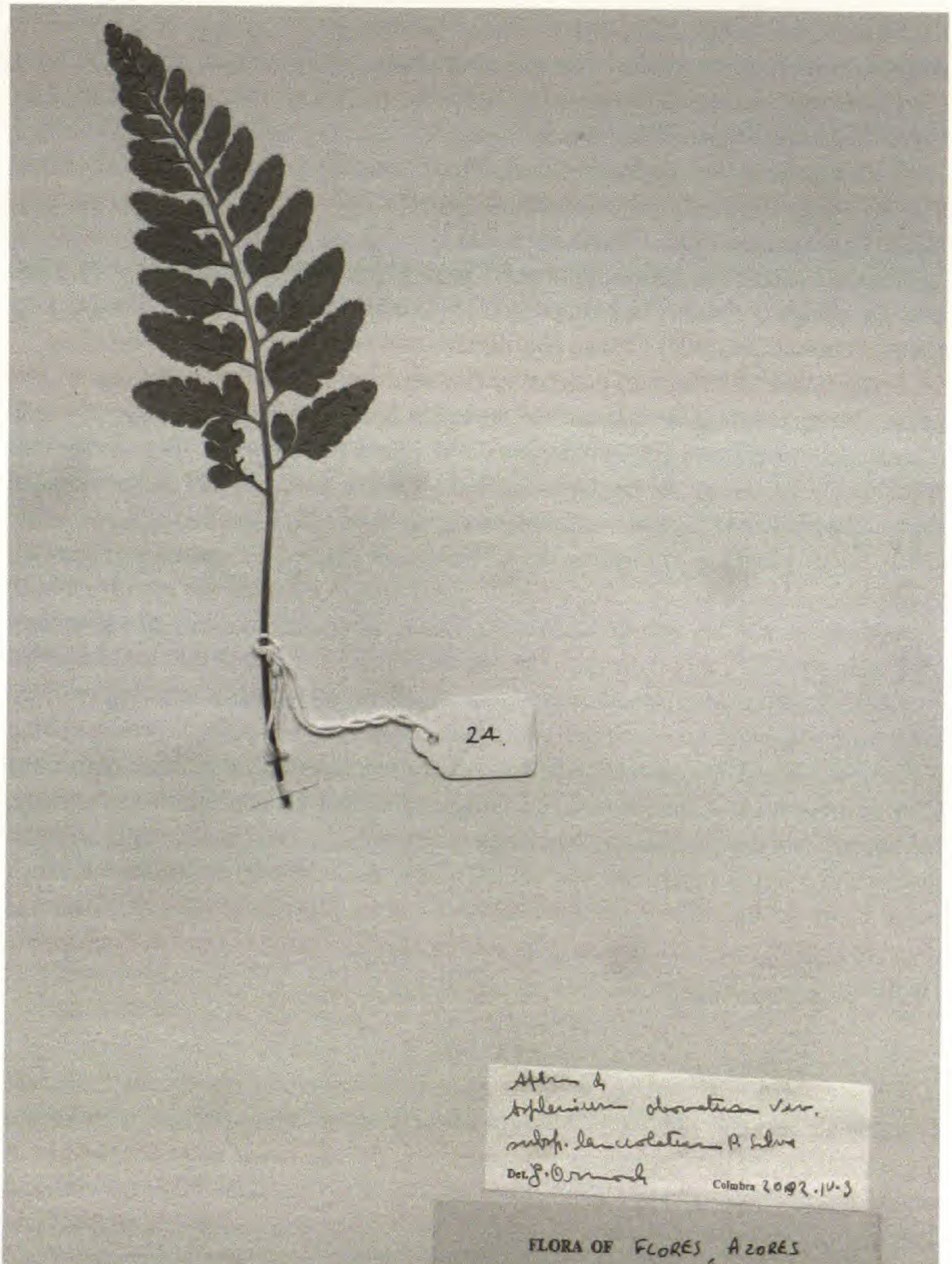

Figure 5. *Asplenium auritum* Sw. – Fajâ Grande, Coada, Flores. C.M. Ward *24*, 2/7/1967. (BM)

Figure 6. *Asplenium auritum* Sw. – Drouet, Flores, 3 Aug. 1857 (BM)

Robba, other species of the genus *Asplenium* and usually roots amongst leafy liverworts such as *Frullania* and *Radula* spp. and various foliose lichens. Plants are also to be found on soil banks adjacent to sections of wall, some of which are now in some disrepair, and on thin soils overlying rocks at the base of the walls. In this it shows considerable similarity to *Asplenium azoricum*, another species believed to have Neotropical affinities but which is far more widely distributed in the archipelago, being found on all of the Azorean islands (Rumsey *et al.*, 2004). In the more exposed sections, higher on walls and with less shade, the plant will regularly experience drought stress (Figure 7) and must show a degree of xerophytic tolerance, although high levels of mortality and turnover are to be expected and are reflected in the observation of numerous juveniles.

CONSERVATION

The Drouet specimen indicates that the species was previously more widespread on Flores and we can record a historical decline in area of occupancy and number of sites. The presence of the species in a zone where the vegetation has seen the greatest change and loss offers the possibility that it was once even more widely distributed or, indeed, may remain to be detected elsewhere. Currently it is effectively restricted to a single site (one contiguous area of habitat under single ownership and management) where is a threat of possible development, and has a small population size (less than 50 mature individuals); together these support Critically Endangered status (CR - B1.a,b; B2a,b;

Figure 7. *Asplenium auritum* Sw. Cuada, Flores, July 2008 – appearance of plant when droughted. Photo. F.J.Rumsey

C2a; D) for the species in the Azores, as defined by the I.U.C.N. (2001).

DISCUSSION

Status and relationships

The Macaronesian region is recognised as a globally important centre for pteridophyte diversity not least because of the high levels of endemicity; just under 10% of the Azorean pteridophyte species are endemic to the archipelago (Vanderpoorten *et al.*, 2011). The biogeography and origins of the taxa on these remote oceanic islands has been the source of interest since initial considerations by Dansereau (1961). The discovery of additional species, and the use of cytogenetics and latterly molecular studies, have revealed more critical differences and helped elucidate floristic affinities. As a consequence, the pteridophyte flora of the Azores has been shown to have a small but distinctive Neotropical or New World element (Vanderpoorten *et al.*, 2007), with the westernmost islands in the archipelago particularly rich in these species, eg. the Grammitidaceae (Schaefer, 2001) and endemic taxa whose closest relatives have been shown to be New World, eg. *Isoëtes azorica* Durieu ex Milde

(Britton & Brunton, 1996) and *Huperzia dentata* (Herter) Holub. The Azorean fern flora shows little affinity to tropical Africa; although some disjunct afro-montane elements are present, these are more of a feature of the more southerly Macaronesian archipelagos (Madeira, the Canaries and Cape Verdes). The endemic taxa are, as with most other described Azorean angiosperm endemics, generally widely distributed across the archipelago (Carine & Schaefer, 2009). The exception, *Marsilea azorica* Launert & Paiva, known only from a single locality, has recently been shown to be synonymous with the Australasian *M. hirsuta* R.Br., a recent invasive weed in tropical North America (Schaefer, Carine & Rumsey, 2011). No single site, or even single island pteridophyte endemic is currently known from the Azorean archipelago, although several non-endemic taxa are restricted to individual sites or islands; this may reflect a comparatively recent arrival, or be as a consequence of ecological (edaphic, biotic or climatic) factors, eg. *Botrychium lunaria* (L.) Sw. recorded only on Pico and restricted to an altitude and environment absent elsewhere in the archipelago.

Biogeographically how should we consider the Azorean *Asplenium auritum*? All evidence points to its being native: restriction to one of the least populous islands, unknown in cultivation and present since some of the earliest periods of exploration of the western islands. While *Asplenium auritum sensu lato* is known from the eastern portion of Southern-most Africa and from Madagascar, the more likely pattern of dispersal is from the Neo-tropics where the species is more abundant. The proof of this assertion will however rely on detailed morphological and molecular studies to elucidate the relationships of these geographically disparate populations. Currently taxonomic treatments and within this group of Spleenworts differ markedly (eg. Proctor, 1985; Adams, 1995; Mickel & Smith, 2004, Roux, 2009; Gabancho, 2011). Many conflicting taxonomic approaches have been taken by recent flora writers working with just a small, local subset of the variation present in the complex. A monographic treatment of the *Asplenium auritum* complex is clearly overdue. Given the wide geographic spread of its occurrences such an undertaking is a challenge to organise and accomplish. Morton & Lellinger (1966) were forced to conclude "until more detailed….studies are made, the division of this complex into taxa based mainly on blade and pinna dissection, blade texture, and spore type will have to stand". Detailed molecular, genetic and micromorphological data are sadly still largely lacking and the circumscription of taxa

and relationships between them, the genomes they contain and the discrete hybridization and polyploid events which have given rise to them, remain to be resolved.

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OBITUARY

Dr Jacobus P. Roux 1954 - 2013

Dr Jacobus P. Roux, or Koos Roux as he was known to all, was curator at the South African National Botanical Institute's (SANBI) Compton Herbarium at Kirstenbosch. Sadly, he was killed in a hit-and-run accident on Sunday 12th May 2013 while out cycling with his son.

Koos' research on ferns was extensive, and included over 40 publications. His first publication, in 1979, was a book, *Cape peninsula ferns*, a very useful guide to the ferns of the area with black and white drawings and a key. He went on to become curator at the Compton Herbarium in the late 1980s, and became a thorough taxonomist, including gaining his PhD in 1998 on a taxonomic revision of *Polystichum*. He published a wide range of papers – new records, descriptions of new species, reviews of genera in Africa or in outlying islands, including *Elaphoglossum*, *Mohria*, *Polystichum* and *Dryopteris*, working from herbarium material, field knowledge and the literature. Eventually he reviewed the whole range of ferns and lycophytes from Africa, culminating in what must be his magnum opus in 2009, *Synopsis of the Lycopodiophyta and Pteridophyta of Africa, Madagascar and neighbouring islands*. This superb volume gives verification of original place of publication of all names, provenance and type localities for names and synonyms, and many names have been lectotypified. The work has 57 new combinations and new names, the introduction gives statistics on numbers of taxa for each individual country or island group, and the book is illustrated with 48 colour pictures. This is the first time the whole fern flora of Africa had been reviewed since Kuhn's publication, *Filices africanae* in 1868. As Koos himself acknowledged, his mammoth task had been greatly assisted through his collaboration with many herbarium curators and fern taxonomists around the world, and the access to on-line scanned type specimens and literature that is now available.

I was delighted when Koos agreed to join the editorial committee of the Fern Gazette in 2012, and he provided several constructive reviews of submitted manuscripts. His untimely death is a huge loss for the Compton Herbarium, for SANBI, and for the ferns of Africa. Titles of his extensive fern publications are listed below. We extend our sympathies to his family and colleagues.

M. Gibby

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SOME NAME CHANGES IN THE PTERIDACEAE OF MACARONESIA AND EUROPE - WITH VALIDATION OF HYBRID NAMES IN THE GENUS *ALLOSORUS* BERNH.

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Key Words: *Allosorus*, *Cheilanthes*, Hybrid, Pteridaceae.

ABSTRACT

Molecular studies have confirmed the polyphyletic nature of the genus *Cheilanthes* Sw. The Macaronesian-Mediterranean taxa form a clade, with Asiatic taxa, distinct from that containing the type *C. micropteris* Sw. and are best recognised as a separate genus for which the earliest available name is *Allosorus* Bernh. The novel species combinations have already been made; those for the nine naturally occurring hybrids currently known between them are validated here.

INTRODUCTION

The large cosmopolitan fern genus *Cheilanthes* Sw. has long been recognised as taxonomically difficult, the recognition of a pragmatic and 'natural' solution to generic circumscription regarded as one of the most contentious issues in fern systematics (Tryon & Tryon, 1982). Molecular phylogenetic studies indicated the polyphyletic nature of this aggregate (Gastony & Rollo, 1995; 1998) and as material from further geographic areas has been studied, eg. Prado *et al.*, 2007; Zhang *et al.*, 2007; Windham *et al.*, 2009, Eiserhardt *et al.*, 2011) polyphyly has been confirmed and interesting bio-geographical patterns clarified. As DNA sequence data accumulates and morphological features are re-examined in the light of molecular phylogenies it becomes possible to recognize monophyletic assemblages of species that can be circumscribed as genera. Ongoing work by Windham and others, eg. Link-Perez *et al.* 2011; Li *et al.* 2012, Grusz & Windham, 2013) has now reached the point with certain groups of cheilanthoid ferns where taxa and clades that cannot reasonably be included within *Cheilanthes* are being circumscribed and named. The examples of the genus from Macaronesia, the Mediterranean, and eastwards to Asia Minor are clearly resolved in a distinct clade (Eiserhardt *et al.*, 2011) separate from that of the New World *C. micropteris* Sw., the nomenclatural type of the genus *Cheilanthes* Sw. Although Grusz & Windham (2013) suggested that as deeper relationships were as yet poorly resolved further evidence might be necessary before generic status was allocated, Christenhusz (2012) took the step of resurrecting the name *Allosorus* Bernh. for this clade.

Allosorus as a genus has had a chequered and controversial nomenclatural history, having been variously interpreted as typified by *Osmunda crispa* L. = *Cryptogramma crispa* (L.) R.Br., *Pteris viridis* Forssk. = *Pellaea viridis* (Forssk.) Prantl and *Adiantum pusillum* Willd. ex Bernh. = *Allosorus pusillus* (Willd. ex Bernh.) Bernh. In each case its application would result, through the rule of priority, in the loss of a much used and familiar generic name (Pichi-Sermolli,1953). Farwell (1931) suggested that the last

interpretation was most appropriate, not only because the majority of species included in Bernhardi's genus are species of *Cheilanthes sensu lato*, but more compellingly, as Pichi-Sermolli (1953) notes, that *Allosorus pusillus* was the only binomial established by Bernhardi (1805) in the genus *Allosorus*.

To preserve the later *Cheilanthes* as the generic name Pichi-Sermolli (1953) proposed the conservation of *Cheilanthes* against *Allosorus*, with *C. micropteris* Sw. as type. This typification has been challenged (Panigrahi, 1987), but was upheld (Lellinger, 1993). When used in a more restrictive sense, as now suggested by the molecular phylogenetic studies, both names are valid and acceptable. Following Pichi-Sermolli (1953) the type of *Allosorus* is *A. pusillus* (Willd. ex Bernh.) Bernh. This has been equated with *Polypodium pteridioides* Reich. = *Allosorus pteridioides* (Reich.) Christenh., which itself has had a confusing and controversial taxonomic history. *Polypodium pteridioides* Reichard was formed as a new name for *Polypodium fragrans* L. (1771), as this was a later homonym for *Polypodium fragrans* L. (1753) = *Dryopteris fragrans* (L.) Schott. The lectotype selected, LINN 1251.34 was however shown to belong not to the tetraploid taxon which had generally gone under the name *Cheilanthes pteridioides* (Reich.) C.Chr. or *C. fragrans* (L.) Sw., but rather the diploid hitherto widely known as *C. maderensis* Lowe (Nardi & Reichstein, 1986). As a consequence a proposal was made to reject the name *Polypodium pteridioides* and all combinations based on it (Nardi & Reichstein, 1986) but this was, following debate, rejected (Pichi-Sermolli, 1987). Bernhardi (1805) equated *Adiantum pusillum* Willd. with *Pteris acrosticha* Balb.; it is likely that Pichi-Sermolli in 1953 would also have equated *Polypodium pteridioides* with this tetraploid taxon, as presumably did Tryon & Tryon, 1982 (as *Cheilanthes fragrans*) before the type of this was shown to belong to the diploid. Examination of original material of *Adiantum pusillum* Willd. ex Bernh. is necessary to confirm the identity, *Allosorus acrosticus* versus *A. pteridioides*, of the generitype.

Christenhusz (2012) made the valid combinations necessary for the species previously recognized in *Cheilanthes* from the Macaronesian and Mediterranean regions, including the creation of a novel specific epithet (*Allosorus fragilis* Christenh.) for the Canarian endemic diploid *Cheilanthes pulchella* Willd., necessitated as the epithet pulchellus was unavailable due to the existence of *Allosorus pulchellus* C.Presl.

For clarity the nomenclatural changes (Table 1) made subsequent to the publication of *Flora Europaea* (Tutin *et al.*, 1993), in which all of the species treated by Christenhusz (2012) (with the exception of the Arabian endemic *Allosorus coriaceus* (Decne) Christenhusz (*Cheilanthes coriacea* Decne)) and other generic changes to taxa which have previously been considered under *Cheilanthes* (eg. Shing, 1993) are presented.

Table 1. Summary of nomenclatural changes in the Pteridaceae of Europe and Macaronesia since the publication of Tutin *et al.*, (1993)

Currently accepted name	Tutin *et al.* (1993) name
Allosorus acrosticus (Balb.) Christenh.	= *Cheilanthes acrostica* (Balbis) Tod.
Allosorus fragilis Christenh.	= *Cheilanthes pulchella* Bory ex Willd.
Allosorus guanchicus (Bolle) Christenh.	= *Cheilanthes guanchica* C.Bolle
Allosorus hispanicus (Mett.) Christenh.	= *Cheilanthes hispanica* Mett.
Allosorus persicus (Bory) Christenh.	= *Cheilanthes persica* (Bory) Mett. ex Kuhn
Allosorus pteridioides (Reichard) Christenh.	= *Cheilanthes maderensis* Lowe
Allosorus tinaei (Tod.) Christenh.	= *Cheilanthes tinaei* Tod.
Paragymnopteris marantae (L.) K.H.Shing	= *Notholaena marantae* (L.) Desv.

Christenhusz (2012) did not, however, provide combinations for the nine naturally occurring hybrids currently known (Rasbach & Reichstein, 1982; Rasbach *et al.*, 1983). That omission is rectified here.

NOVEL COMBINATIONS

Allosorus* × *ibericus (Rasbach & Reichst.) F.J.Rumsey, **comb. nov.** ≡ *Cheilanthes* × *iberica* Rasbach & Reichst. in Webbia 35(2):264. 1982.
[*Allosorus hispanicus* (Mett.) Christenh. × *A. tinaei* (Tod.) Christenh.]

Allosorus* × *insularis (Rasbach & Reichst.) F.J.Rumsey, **comb. nov.** ≡ *Cheilanthes* × *insularis* Rasbach & Reichst. in Webbia 35(2):266. 1982.
[*Allosorus guanchicus* (Bolle) Christenh. × *A. tinaei* (Tod.) Christenh.]

Allosorus* × *kochianus (Rasbach, Reichst. & Schneller) F.J.Rumsey, **comb. nov.** ≡ *Cheilanthes* × *kochiana* Rasbach, Reichst. & Schneller in Webbia 37(1):48. 1983.
[*Allosorus pteridioides* (Reichard) Christenh. × *A. tinaei* (Tod.) Christenh.]

Allosorus* × *kurdicus (Rasbach, Reichst. & Schneller) F.J.Rumsey, **comb. nov.** ≡ *Cheilanthes* × *kurdica* Rasbach, Reichst. & Schneller in Webbia 37(1):58. 1983.
[*Allosorus acrosticus* (Balb.) Christenh. × *A. persicus* (Bory) Christenh.]

Allosorus* × *malacitensis (Rasbach & Reichst.) F.J.Rumsey, **comb. nov.** ≡ *Cheilanthes* × *malacitensis* Rasbach & Reichst. in Webbia 35(2):269. 1982.
[*Allosorus acrosticus* (Balb.) Christenh. × *A. guanchicus* (Bolle) Christenh.]

Allosorus* × *marchettianus (Rasbach, Reichst. & Schneller) F.J.Rumsey, **comb. nov.** ≡ *Cheilanthes* × *marchettiana* Rasbach, Reichst. & Schneller in Webbia 37(1):55. 1983.
[*Allosorus acrosticus* (Balb.) Christenh. × *A. pteridioides* (Reichard) Christenh.]

Allosorus* × *prototinaei (Rasbach, Reichst. & Schneller) F.J.Rumsey, **comb. nov.** ≡ *Cheilanthes* × *prototinaei* Rasbach, Reichst. & Schneller in Webbia 37(1):45. 1983.
[*Allosorus hispanicus* (Mett.) Christenh. × *A. tinaei* (Tod.) Christenh.]

Allosorus* × *teneriffae (Rasbach & Reichst.) F.J.Rumsey, **comb. nov.** ≡ *Cheilanthes* × *teneriffae* Rasbach & Reichst. in Webbia 35(2):264. 1982.
[*Allosorus fragilis* Christenh. × *A. pteridioides* (Reichard) Christenh.]

Allosorus* × *tolocensis (Rasbach, Reichst. & Schneller) F.J.Rumsey, **comb. nov.** ≡ *Cheilanthes* × *tolocensis* Rasbach, Reichst. & Schneller in Webbia 37(1):52. 1983.
[*Allosorus guanchicus* (Bolle) Christenh. × *A. pteridioides* (Reichard) Christenh.]

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INSTRUCTIONS FOR AUTHORS

PAPERS should not usually exceed 20 printed pages and are generally expected to be considerably shorter. As well as reports of original research, review articles and short notes, e.g. new records, are encouraged. The senior author should supply an email address to facilitate correspondence.

REVIEWS should cover recent developments in any aspect of research on ferns and lycopods. This can include unpublished research by the author, and/or the possible direction of future research. They should be aimed at the general reader who may not be an expert in the chosen topic. Proposals for a review should be discussed first with the review editors.

MANUSCRIPTS should be submitted in English (British) in electronic format in 10-point Times New Roman font and double spaced. Electronic versions of text and tables should be compatible with WORD, with figures as pdf or jpg files, and sent as email attachments or CDroms. All manuscripts will be refereed.

THE TITLE should reflect the content of the paper and be in BOLD CAPITALS (11-point) and centrally aligned. Generic and specific names should be in italics and any title containing a generic or specific name should be followed by the family name in brackets e.g.

***TRICHOMANES SPECIOSUM* (HYMENOPHYLLACEAE) IN SOUTHERN SPAIN**

AUTHOR ABBREVIATIONS should follow Pichi Sermolli's (1996) Authors of scientific names in Pteridophyta, Royal Botanic Gardens, Kew.

MAIN HEADINGS: should be in **BOLD CAPITALS** (10-point) and centrally aligned.

SUBSIDIARY HEADINGS: should be in **bold**, the first letter of each word in capitals, the rest in lower case and left-aligned.

AUTHORS' NAMES AND FULL ADDRESSES (including email address): follow the title and are centrally aligned.

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STEVENSON, D.W. & LOCONTE, H. 1996. Ordinal and familial relationships of pteridophyte genera. In: CAMUS, J.M., GIBBY, M. & JOHNS, R.J. (Eds) Pteridology in perspective, pp. 435-467. Royal Botanic Gardens, Kew.

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CONTENTS

REVIEW

Biogeography of the Brazilian Atlantic forest: evidence from phylogenetic data sets and perspectives for fern and lycophyte studies
J. Prado & R.Y. Hirai 241-257

A short biography of the authors 258

MAIN ARTICLES

***Asplenium auritum* Sw. *sensu lato* (Aspleniaceae: Pteridophyta) - an overlooked Neotropical fern native to the Azores**
F.J. Rumsey, H. Schaefer & M. Carine 259-271

Some name changes in the Pteridaceae of Macaronesia and Europe - with validation of hybrid names in the genus *Allosorus* Bernh.
F.J. Rumsey 275-279

OBITUARY

Dr Jacobus P. Roux
M. Gibby 272-274

INSTRUCTIONS FOR AUTHORS 280

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